

A new species of *Mabuya* (Sauria: Scincidae) from the British Virgin Islands

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Abstract.—*Mabuya macleani*, new species, is a pallid, drab, almost patternless skink which is abundant on Carrot Rock, British Virgin Islands. *Mabuya sloanii* shows character divergence in pattern from the new species concordant with geographic approach to within 400 m. On Puerto Rico, *M. sloanii* has a broad middorsal bronzy area on the anterior dorsum. On most of the smaller islands of the Puerto Rico Bank, as well as the Mona and Desecheo Banks to the west, this middorsal area is much narrowed by the presence of well-developed dark dorsolateral stripes stretching from the head to behind the forelimbs. These two pattern types, which apparently intergrade in the vicinity of northeasternmost Puerto Rico, are recognized as *M. s. nitida* Garman and *M. s. sloanii* Daudin, respectively. The specific name "mabouya" Lacépède, formerly applied to Antillean skinks, is shown to be unavailable. The presence of *M. macleani* and another endemic lizard (*Anolis ernestwilliamsi*) on such a small (1.3 ha), poorly isolated, and young (<3000 y) island as Carrot Rock may be a striking case of rapid divergence of insular populations.

"The coloration is highly interesting . . . several insular forms may be distinguishable when adequate series become available." Karl P. Schmidt (1928)

The scincid lizards of the genus *Mabuya* are nearly tropicopolitan in distribution. We have collected or examined them in numbers from the Antilles, South America, tropical Asia, and Africa. Throughout this vast range, most species are brown with near-black stripes extending the length of the body. A striking exception is on Carrot Rock, a very small (1.3 ha), steep-sided island off the southeast end of Peter Island in the British Virgin Islands (Fig. 1).

On 13 July 1985, while one of us (GCM) climbed the biggest tree on the island in search of anoles, the other (JL) toiled in the dust in the little gully on the windward side of Carrot Rock in which the tree grew, looking for *Sphaerodactylus* geckos. A far larger, drab, pale lizard was turned out, and ran up his sleeve. Although this initial spec-

imen was distinctive, we at first referred to it as *Mabuya mabouya sloanii* (Mayer & Lazell 1988), the common skink of the Virgin Islands (MacLean 1982, Lazell 1983), pending collection of further specimens. Over the next several years JL returned to Carrot Rock occasionally, and found an area where these peculiar pallid lizards were abundant, and succeeded in capturing five more individuals (of dozens seen). These specimens, as well as comparison with *Mabuya* from throughout the islands of the Puerto Rican Bank, have abundantly confirmed the distinctiveness of this population, and also brought into sharp focus a most intriguing evolutionary phenomenon. We here describe this distinctive *Mabuya* as:

Mabuya macleani, new species

Mabuya mabouya sloanii.—Mayer & Lazell, 1988:23 (in part).



Fig. 1. Carrot Rock, British Virgin Islands, viewed from the north, 17 July 1988. Windward is to the left, leeward to the right. The highest elevation is ca. 25 m. From a Kodachrome transparency by GCM.

Holotype.—Museum of Comparative Zoology (MCZ) 170884, collected on Carrot Rock, south of Peter Island, British Virgin Islands, 18°19'45"N, 64°34'18"W, by J. Lazell, 13 Jul 1985 (Fig. 2D).

Paratypes.—All from the type locality: MCZ 182270–72, 17 Jul 1988; MCZ 176728 and University of Michigan Museum of Zoology (UMMZ) 197261, both 26 Oct 1991.

Diagnosis.—A pallid tan to brownish-gray New World *Mabuya* (Dunn 1936, Greer 1970) with one or two pairs of enlarged nuchals (their combined widths more than 75 percent of the width of the parietals); two frontoparietals; parietal overlapping upper anterior temporal (Greer & Nussbaum 2000); midbody scales in 32–34 rows; 16–18 subdigital lamellae under fourth toe of pes; limbs moderately long; dark dorsal markings fragmented or absent on head and separated from dark dorsolateral stripes on nape; nape stripes reduced, separated by all or most of two dorsal scales and not extending more than 21 dorsal scales posterior to parietals; lateral dark stripes poorly developed. *Mabuya macleani*

is distinguished from the geographically nearest populations of *M. sloanii* by the much reduced dorsolateral dark stripe, the continuous stripe beginning behind the head in *M. macleani* (on the head in *M. sloanii*), and extending only to the level of the forelimbs (behind the forelimbs in *M. sloanii*).

Description of the type.—Rostral wider than high, bordered dorsoposteriorly by the nasals and paired supranasals, which are in narrow contact. The frontonasal is broader than long and in contact with the frontal. The paired prefrontals are separated medially by the contact of the frontonasal with the frontal. The frontal is about three quarters as long as its distance from the posterior parietal edge. There are four supraoculars, the second the largest. There are three supraciliaries, the first by far the longest. The two frontoparietals are in contact with the second, third, and fourth supraoculars, bordered posterolaterally by the parietals, and posteriorly by the interparietal, in which the parietal foramen is posteriorly situated. The large, paired parietals are in contact posterior to the interparietal, that on

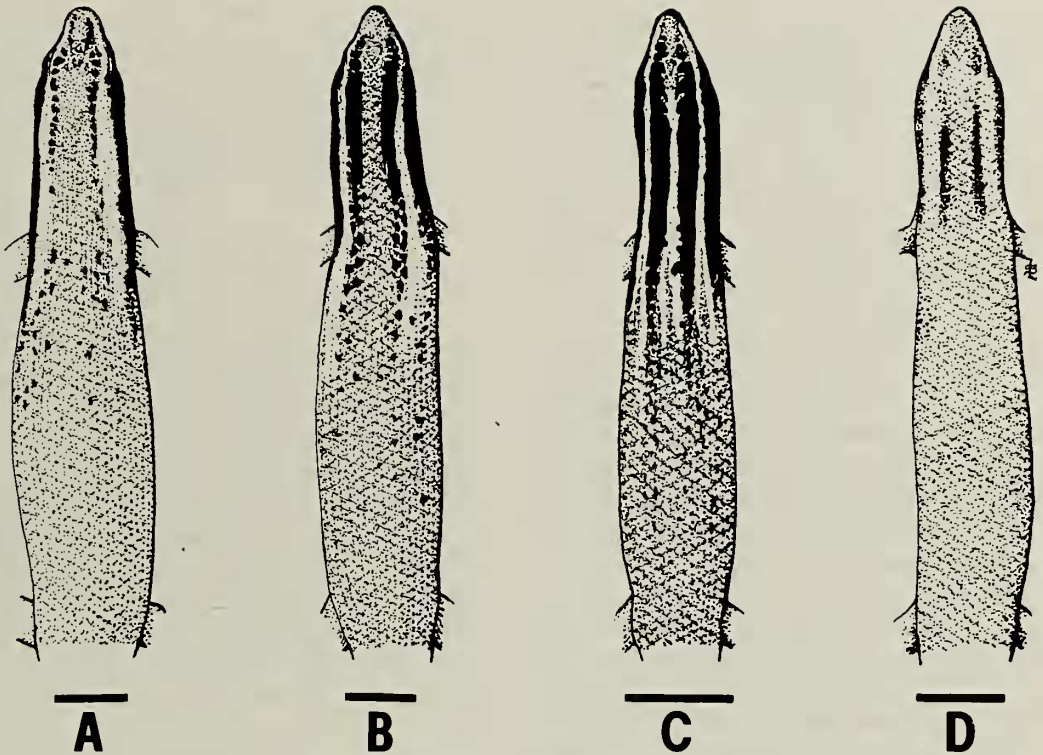


Fig. 2. Dorsal patterns of skinks from the Puerto Rican Bank. A–C, geographically approaching Carrot Rock: A) MCZ 6050, lectotype of *Mabuya sloanii nitida*, San Juan, Puerto Rico, ca 164 km WNW of Carrot Rock. B) MCZ 36624, intergrade, *M. s. nitida* × *sloanii*, Cayo Icacos, ca. 102 km WNW of Carrot Rock. C) MCZ 182273, *M. s. sloanii*, Stoney Bay, Peter Island, British Virgin Islands, 400 m N of Carrot Rock. D) MCZ 170884, type of *Mabuya macleani*, Carrot Rock, British Virgin Islands. Bars below lizards indicate 1 cm in each case.

the right extending further posteriorly. The parietals overlap the upper anterior temporal. There is one pair of transversely enlarged nuchals, but the second and third nuchals are enlarged on the left side.

The nasal is subrectangular in side view, with the large nostril posteriorly located, followed by the postnasal and two loreals; the anterior one on the left is much larger than the posterior, but the two are subequal on the right. The anterior loreal is in contact with the prefrontal, but the posterior loreal is separated from the latter scale by a presupraciliary. The sixth supralabial on the left, and the fifth on the right, are about twice as long as the others, the enlarged supralabial on each side forming a long subocular. There is a clear disk in the lower

eyelid about as wide as the ear opening. The temporals are larger than the trunk scales. There are no auricular denticles. There are two pairs of chin shields in contact posterior to the mental.

Scales of body and limbs imbricating, subcycloid, regularly arranged in rows. Thirty-four longitudinal rows at midbody, 57 transverse rows dorsally from parietals to anterior edge of hind limb, 61 ventrally from mental to vent. The vent is bordered anteriorly by eight subequal scales. Scales of soles and palms tubercular, transition from imbricate scales of limb to tubercular scales abrupt. Thirteen lamellae under fourth toe of manus, 17 under fourth toe of pes. Adpressed limbs do not meet.

In life, the type was pallid beige-gray

Table 1.—Some characteristics of *Mabuya macleani*. "Scales" are number of rows around trunk at midbody. "Stripe" is the length of the dorsolateral dark stripe in dorsal scales posterior to the parietals (left/right).

	SVL	Scales	Supra-nasals	Stripe	Nuchal Pairs	Adpressed limbs
MCZ 170884	69.5	34	Contact	15/16	1	Fail to meet
MCZ 176728	71.0	32	Contact	18/18	1	Toes barely touch
MCZ 182270	80.5	32	Contact	17/18	2	Fail to meet
MCZ 182271	76.0	32	Contact	18/15	1	Fail to meet
MCZ 182272	63.0	32	Separated	17/18	2	Meet
UMMZ 197261	44.5	32	Fused	21/21	1	Toes overlap

with a faint trace of a lateral stripe extending to just above the axilla. There are two dark dots on the frontonasal and a little dark gray flecking on the supraoculars. The plain lead-gray dark dorsolateral stripes end 15 (left) or 16 (right) dorsal scales posterior to the parietals.

Variation.—Some characteristics of *Mabuya macleani* are given in Table 1, and measurements in Table 2. The holotype is fairly typical of the type series in its squamation, and the paratypes do not present a great deal of variability. Dorsal and ventral head scales of MCZ 182270 are shown in Fig. 3. This specimen shows two unusual conditions: the presence of an intercalary scale separating the first supraocular from contact with the frontal on the left side of the head, and the partial fusion of the fourth

supraocular with the parietal, also on the left side. Contact of the supranasals is variable, being separated in one specimen, touching in four, and even fused medially into a single scale in another. The prefrontals are never in contact medially. In lateral view, the head squamation of *M. macleani* is essentially similar to that of *M. sloanii* shown by Schmidt (1928:122).

The following summary of meristic variation gives for each character the range, followed by the mean and sample size in parentheses. For some bilateral characters the sample size has been reckoned by the number of sides rather than specimens, and this is noted after the sample size. Supraoculars: 4 (4.0, 12 sides); supraciliaries: 2–4 (3.0, 6 sides); supralabial subtending the eye (subocular): 5–6 (5.3, 11 sides); mid-

Table 2.—Measurements (mm) of holotype and three paratypes of *Mabuya macleani*.

	MCZ 170884 Holotype	MCZ 182270 Paratype	MCZ 182271 Paratype	MCZ 182272 Paratype
Snout-vent length	69.5	80.5	76.0	63.0
Tail length	52+	67+	56+	75.5
Axilla-groin length	38.0	45.0	40.5	34.5
Snout length	5.4	5.7	5.7	5.0
Snout width	5.5	5.5	5.4	4.9
Head length	11.9	13.0	12.8	11.4
Head width	8.2	10.2	10.2	8.0
Upper arm length	5.5	6.5	6.0	5.0
Lower arm length	4.9	5.5	6.5	4.7
Palm length	1.9	2.8	2.6	2.9
Fourth finger length	4.5	4.5	4.5	4.0
Upper leg length	8.0	8.0	8.0	7.0
Lower leg length	6.6	7.5	7.3	6.6
Sole length	3.4	3.8	4.3	3.1
Fourth toe length	6.5	7.0	7.0	7.5

+ Tail broken or regenerated.

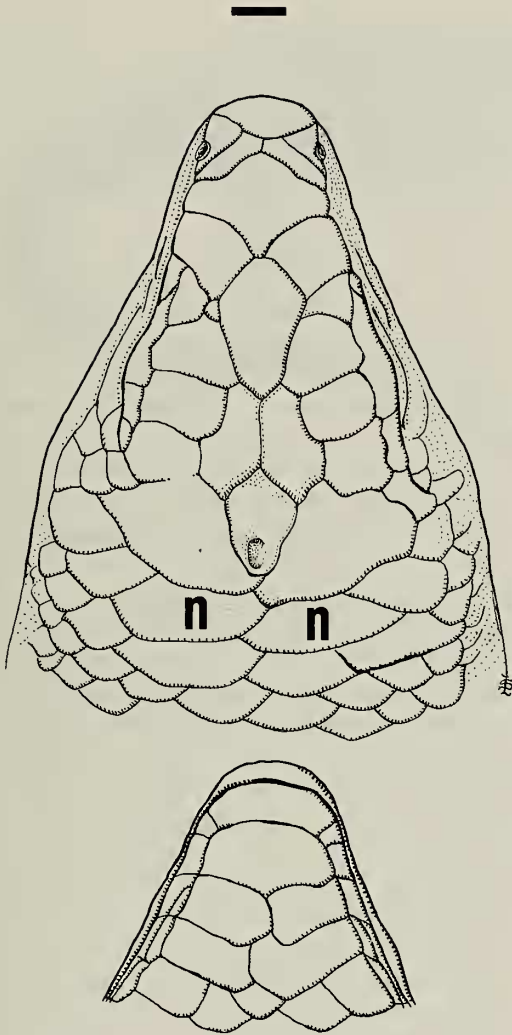


Fig. 3. Aspects of head squamation in MCZ 182770, *Mabuya macleani* paratype. The first pair of enlarged nuchals are marked "n." Bar is 1 mm.

body scale rows: 32–34 (32.3, 6); transverse dorsal rows: 54–58 (56.0, 4); transverse ventral rows: 58–66 (61.2, 6); fourth toe of manus lamellae: 13 (13.0, 4); fourth toe of pes lamellae: 16–18 (17.2, 5).

All *Mabuya macleani* have a much reduced pattern of striping compared to the near-black striping typical of Antillean *Mabuya* (Fig. 2), but the extent of reduction varies, and seems to be size related, with smaller specimens having less reduced markings. All specimens of *M. macleani*

have paired blotches on the frontonasal, but they are scarcely evident on the largest specimen (MCZ 182270), in which, were it not for their presence in the other specimens, they might be taken to be merely two of several scattered dark mottlings on the head, rather than reduced pattern elements. In all specimens the dorsolateral stripe is short and starts on the neck, beginning 3–5 (4.6, 12 sides) scales behind the parietals, and extending to the 15th to 21st (17.7, 12 sides) transverse dorsal scale row behind the parietals; the posterior end is thus at about the level of the forelimbs. There is also size related variation in the intensity of the striping, the dorsolateral dark and light stripes being relatively darker and lighter, respectively, in the second smallest specimen (MCZ 182272) than in the larger ones. The most distinctive pattern variation is in the smallest specimen (UMMZ 197261), which, in addition to the frontonasal blotches and dorsolateral dark stripe (which is longest in this specimen, extending from the 5th to 21st scale row), also has two short stripes on the head, extending from the second supraoculars to the parietals.

There appears to be allometric growth of the limbs. The smallest individual, UMMZ 197261, 44.5 mm SVL, has proportionately by far the longest limbs, and MCZ 187220, 80.5 mm SVL, the largest, has the shortest. The other four are intermediate. The type, at 69.5 mm SVL, has slightly shorter limbs proportionately than MCZ 176728, 71 mm SVL, but the overall impression is that limb length fails to keep pace with body growth. In studies of other New World *Mabuya*, based on larger series than available of *M. macleani*, a similar decline in relative limb length has been demonstrated: Rebouças-Spieker (1974) found this to be the case for most samples in her study of *M. agilis*, *M. caissara*, and *M. macrorhyncha*; Rebouças-Spieker & Vanzolini (1990) found it in *M. carvalhoi*; and Avila-Pires (1995) found it in *M. bistrriata* (= *ficta* sensu Rebouças-Spieker) and *M. nigropunctata* (= *bistrriata* sensu Rebouças-Spieker).

The sexes are similar. Based on broad head, thick tail base, and enlargement of the medial pair of scales bordering the vent, MCZ 182271 was judged to be a male, and dissection confirmed that. Based on narrow head, abruptly tapering tail, and subequal scales bordering the vent, MCZ 187220, the largest available specimen, was judged to be a female, and dissection confirmed that.

Comparisons.—*Mabuya macleani* is morphologically and geographically closest to *M. sloanii*. The latter species is widespread, but nowhere abundant, in the Passage and Virgin Islands, and is also found on Mona and Desecheo (Heatwole et al. 1981, Lazell 1983, 1991, 1995; Mayer 1989). This skink is deep copper to chocolate brown with prominent lateral stripes of near-black and very bold jet black dorsolateral stripes, beginning on the head, and extending continuously down the nape onto the anterior trunk, well past 20 dorsal scales posterior to the parietals (Figs. 2C, 4). The dark dorsolateral stripes are black and separated by silvery-white on the median portions of the two middorsal scale rows. On Puerto Rico, skinks also have near-black lateral stripes extending onto the trunk, but the dark dorsolateral stripes are reduced to heavy blackish blotching on the head, fragmenting and dwindling to speckles on the nape (Fig. 2A). This pattern form was named *M. nitida* by Garman (1887) on the basis of one specimen from Hispaniola and three from Puerto Rico. Stejneger (1904) described this form accurately, mistakenly under the name *M. sloanii*, based on one of two specimens numbered MCZ 6052 from San Juan, Puerto Rico. He also noted the existence of the other pattern type (the actual *sloanii*) under the name *semitaeniata* Wiegmann (1837). Schmidt (1928) also noted the two patterns, and restricted Garman's *nitida* to Puerto Rico. Grant (1931) recognized the distinction in pattern between the Puerto Rican and small island forms as well, using the same erroneous names as did Stejneger. Six Puerto Rican specimens available to us, from San Juan

(MCZ 6050, MCZ 6052 [2 specimens]), Ensenada (American Museum of Natural History [AMNH] 6462), and Bayamon (AMNH 14007, UMMZ 73828) agree with Schmidt and Stejneger's descriptions, as did the Puerto Rican specimens available to Grant (1931).

A seventh specimen, from easternmost Puerto Rico (UMMZ 73829, Cape San Juan), shows some approach toward the *sloanii* pattern. A specimen from Icacos (MCZ 36624), an island just east of Puerto Rico, is intermediate between *nitida* and *sloanii* of the smaller islands to the east (Fig. 2B). Based on these specimens and the literature, we recognize *M. s. nitida* as a valid taxon, and confirm Schmidt's restriction of type locality by selecting MCZ 6050 as the lectotype. A similar pattern of geographic variation, with a Puerto Rican mainland form and a Passage/Virgin Islands form showing signs of intergradation in easternmost Puerto Rico and the adjoining cays is found in *Anolis cristatellus* (Heatwole 1976). It is interesting that *s. sloanii* occupies the islands to the east and west of the Puerto Rican main, with *s. nitida* occupying the main in between; a similar Puerto Rican distribution is shown by *Hemidactylus mabouia* (Kluge 1969) and *Epicrates monensis* (Schwartz & Henderson 1991), with related species on the Puerto Rican main (*H. brookii* and *E. inornatus*).

The overall picture is of Puerto Rico Bank *Mabuya sloanii* showing greater character divergence from *M. macleani* as the latter's geographic distribution is approached (Figs. 2, 5). *Mabuya s. nitida* has less dark anterodorsal pigment than does *M. s. sloanii*; however, *M. s. sloanii* occurs to within 400 m of *M. macleani*, but the latter has the least dark pigment of all.

The Caicos Islands, although geologically part of the Bahamas, share a number of herpetofaunal elements with the Puerto Rico Bank (*Anolis*, *Typhlops*—Thomas 1999). The skinks of these islands appear distinct from Puerto Rico Bank ones based on the specimens we have seen. We have

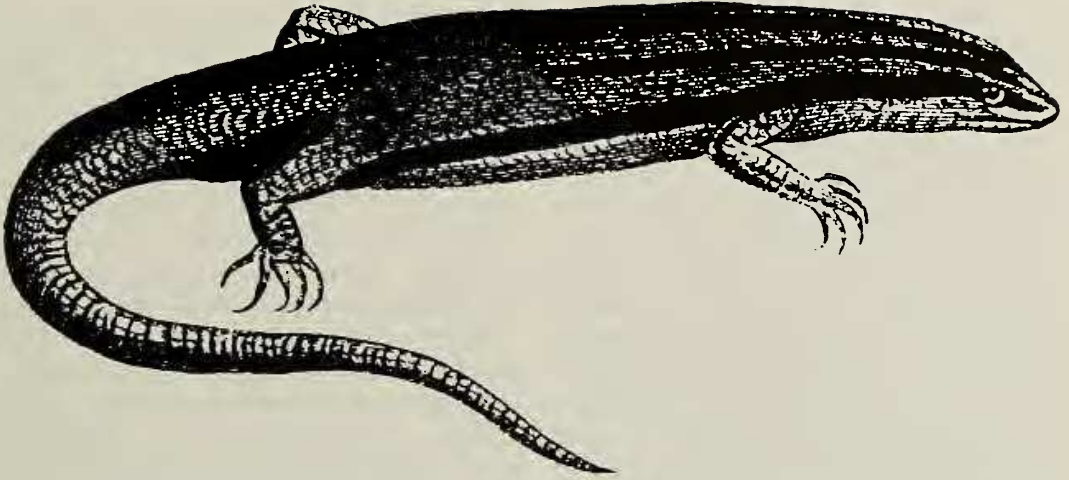


Fig. 4. Daudin's (1802) illustration of his *Scincus sloanii*, the widespread form of the Virgin Islands, showing pattern in side view.

color notes in life for MCZ 182881 from Long Cay, Caicos Bank: dark bronze-brown dorsally, with two very bold cream-white stripes that begin at the snout and ex-

tend dorsolaterally onto the costal region, about one-third of the distance from axilla to groin; these light stripes are bordered ventrally by a near-black field, six scale

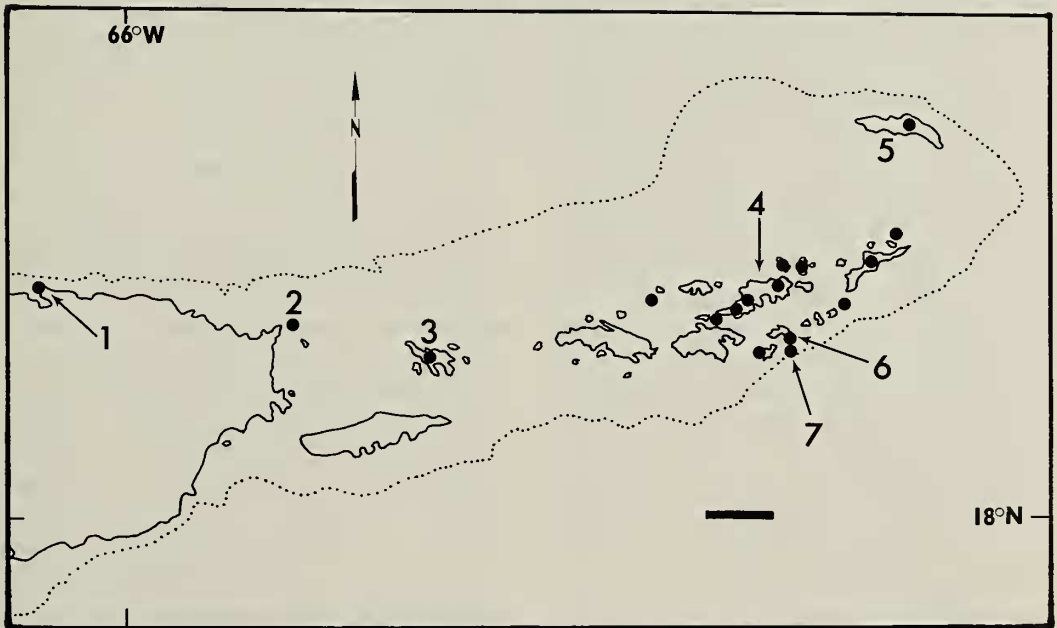


Fig. 5. The eastern portion of the Puerto Rico Bank showing localities from which specimens have been examined. 1, San Juan, Puerto Rico, type locality for *Mabuya sloanii nitida*. 2, Cayo Icaicos, represented by an apparent *M. s. sloanii* × *nitida* intergrade. 3, Isla Culebra, 4, Tortola, 5, Anegada, 6, Peter Island, all nominate *M. s. sloanii*. 7, Carrot Rock, type locality for *Mabuya macleani*. Bar indicates 10 km. The dotted line is the edge of the Puerto Rican Bank, ca. 100 m below sea level.

rows wide at the forelimb insertion, and flecked with white speckles. The light dorsolateral stripes are bordered dorsally by near-black stripes one scale wide at the forelimb insertion and separated by four scales across the dorsum at that level. The posterior body is heavily speckled with black dots aligned in longitudinal rows. A preserved series from the same island (AMNH 80125–30) agrees well in pattern with the live specimen described above. The striping pattern most resembles that of the Icacos intergrade (Fig. 2B), except that the middorsal brown area is about twice as wide, thus being more like *nitida*, but differing from the latter in having a broader dorsolateral dark stripe, and in that the Icacos specimen lacks the heavy, aligned body spotting of the Caicos specimens. Such spotting is variable in *M. s. sloanii*, and may be fairly heavy (Grant 1931; UMMZ 80585 [Buck Island off St. Thomas]). White speckling in the lateral dark stripe, which is also seen in specimens from West Caicos (UMMZ 117392–4) and Six Hill Cays (UMMZ 117394–6), is not found in Puerto Rican region specimens. Further study, beyond the scope of the present work, may reveal that the Caicos *Mabuya* should be recognized as a valid taxon.

Dunn's (1936) description of *Mabuya pergravis* of the western Caribbean, "striping very indistinct; pale with dark dots above," may sound superficially similar to *M. macleani*, but the two forms are amply distinct. *Mabuya pergravis* is much more slender, and has fewer midbody scale rows (28–30—Dunn 1936, Dunn & Saxe 1950). Striping is not indistinct in a single specimen from San Andrés, and in those from Providencia the dark dots are numerous (unlike *macleani*, in which there are few or no dark dots dorsally).

In meristic and measurable characters, all New World *Mabuya*, and most from the rest of the world, are slightly, and often only modally, differentiated; as Greer & Nussbaum (2000) noted, "Few unequivocal characters of scalation are available." *Ma-*

buya macleani differs from *M. sloanii* somewhat in having smaller scales, reflected in higher midbody row counts: 32–34, as opposed to 30–32 in other Puerto Rico Bank *Mabuya* ($n = 20$). It would take larger sample sizes to even demonstrate statistical significance. There may be selection pressure for smaller scales in *M. macleani*. Carrot Rock's other endemic lizard, *Anolis ernestwilliamsi*, has very small scales and is absolutely distinct from its closest relative in this character (Lazell 1983). Interpreting the adaptive significance of scale size in lizards is, however, fraught with difficulties and apparent contradictions (Lazell 1994, Dmi'el et al. 1997).

Etymology.—The species is named in honor of our late friend and colleague Dr. William P. MacLean, III, of the University of the Virgin Islands, who contributed so much to knowledge of the Virgin Island herpetofauna (MacLean 1982), and who aided and assisted our work, and that of many others, on numerous occasions (Lazell & Mayer 1992). He was one of the first, and still few, professional biologists ever to have set foot upon Carrot Rock, and recognize its biotic uniqueness.

Discussion

Ecology.—Carrot Rock has undergone major ecological changes since it was first visited by JL in 1980 (Lazell 1983). Then, most of the windward (eastern) and northern portion of the top of the island was covered with a sprawling growth of sea grape, *Coccoloba uvifera* (Polygonaceae), which had to be either climbed over or crawled under. There were three thickets of sea grape on the edges of the scarp tall enough to stand in the shade of: one on the leeward coast, one on the northern windward coast, and the biggest in the gully—locally called "ghut"—where the first *Mabuya macleani* was collected.

Severe drought characterized the climate of the Virgin Islands during the eighties. It seemed that more precipitation fell in the

form of dust—said to have blown all the way from the Sahara—than as water. JL's field notes of 13 July 1985 record:

“The Rock is in terrible shape! The sea grape looks 90% dead; places I could crawl under before are now just scattered dry sticks. Trying to dig out leaf litter was a nightmare of dust.”

Despite the drought, *Anolis* remained common, the first *Mabuya* was secured, and *Sphaerodactylus macrolepis* (MCZ 170890) was also collected—all in the one remaining sea grape thicket in the ghut—in 1985 (Mayer & Lazell 1988). This brought Carrot Rock into compliance with the “rule of three” for Caribbean islands, as predicted (Lazell 1983). On 17 July 1988 conditions were no better, but more *M. macleani* were seen and collected than ever before. Over most of the boulder-jumbled surface of Carrot Rock, skinks have the advantage over would-be captors. In one small area near the top, however, there are few rocks, little vegetation, and a soil substrate. Here a group of us simultaneously sighted eight skinks in a 10 × 20 m (200 m²) plot (and caught three of the eight). Excluding the bare rock faces and wave-washed talus of the edges, we estimate the top of the island habitable for skinks at ca. 1.3 ha. Using our crude estimate, the total population of *Mabuya macleani* might be something like 520 individuals. In any case, a density of 12 in 200 m² (400 per ha) far exceeds that of skinks or other comparable ground lizards (e.g., *Ameiva*) anywhere in the Antilles.

On 27 October 1994, three *Mabuya macleani* were seen in about two hours on the Rock. JL's field notes mention “the incredible drought,” and the appearance of the island as “dead gray still” and “really bleak.” Hurricanes Luis and Marilyn struck the Virgin Islands in September 1995. Low-lying areas like Carrot Rock were inundated with sea water, but there was relatively little mitigating rainfall. On this day the Rock was visited with a group of 6 people, but in two hours ashore we saw but two skinks and not a single *Anolis*. Approximately half

the sea grapes in the ghut thicket were dead. The large candelabra cactus, *Pilosocereus royenii*, that had crowned the top of the islet (and housed the largest, uncatchable *Anolis*) was “rotting pulp and stark skeleton.”

Rainfall in the region began to increase in 1996. On 24 October 1996 a group of us checked the Rock briefly. We did not attempt to collect specimens, but we quickly located three *Anolis ernestwilliamsi* and two *Mabuya macleani*, one of the latter perched on a vine ca. 3 cm above the ground (Schwartz & Henderson [1991] note climbing in *Mabuya mabouya*). Again, from JL's field notes: “Seagrapes are regenerating well; the place generally looks much better than last year.”

A brief vegetation survey of Carrot Rock, by Dr. Fred Kraus on 26 October 1991, included, in addition to seagrape and candelabra cactus, *Mammillaria nivosa*, *Melocactus intortus*, and *Opuntia dillenii* (all Cactaceae), and the vines *Capparis flexuosa* (Capparidaceae), *Stigmaphyllon periplocifolium* (Malpighiaceae), and *Cavanalia maritima* (Leguminosae). There are “various graminoids including the rare silky foxtail grass *Pappophorum pappiferum*.”

Differentiation on small islands.—The distinctiveness of populations inhabiting small islands, and the apparently rapid evolutionary rates involved in achieving this differentiation, have long been known to students of the zoology of archipelagos (Mayr 1963, Lazell 1972). *Mabuya macleani* appears to be an example of this phenomenon. Two aspects of Carrot Rock's geographic situation, in particular, argue for rapid evolution (Fig. 6). First is its short distance, approximately 400 m, from Peter Island. Given this short distance, and the predominant direction of the currents from the northeast, there seems a considerable probability of waif dispersal of skinks from adjacent parts of Peter Island (where typical *M. sloanii* does occur: MCZ 182273) or other islands to windward. Divergence of the Carrot Rock population, especially by

genetic drift, would have to proceed at a high rate to offset the genetically homogenizing effects of immigration events.

The second aspect is the short time during which Carrot Rock has existed as a separate island. Lowered sea levels during the last glacial period united all of the islands of the Puerto Rico Bank into a single large island (Heatwole & MacKenzie 1967). The age of separation of two islands on the bank can be inferred from the maximum depth of the water now separating them, and the time course of the Holocene sea level rise. We cannot say with certainty what the maximum depth of the channel between Carrot Rock and Peter Island is, because the channel is so shallow and strewn with rocks that only the smallest of boats attempt to pass through the strait, so that accurate soundings are not possible; it cannot be more than a few meters. Based on the time course of Caribbean sea level rise (Fairbanks 1989), a depth of 5 m would correspond to a separation of 3000 years; as the actual depth is almost certainly less than this, this is an upper limit on the time of isolation of Carrot Rock.

The causes of rapid divergence in island populations have long been a matter of contention (Williamson 1981, Berry 1986, Grant 1998), with some arguing for the importance of stochastic factors (e.g., Mayr 1954), while others have stressed the adaptive nature of island differentiation (e.g., Grant 1968, Malhotra & Thorpe 2000). Carrot Rock's proximity to Peter Island argues for a non-stochastic cause, since even a low rate of migration is sufficient to counteract divergence due to founder effect or drift (Crow and Kimura 1970); gene flow is much less effective in counteracting selection (Lande 1980). There is another, in our opinion much stronger, argument for non-stochastic causes: the occurrence on Carrot Rock of another endemic lizard, *Anolis ernestwilliamsi*, which, like *Mabuya macleani*, has a close relative, *A. cristatellus*, widespread on other islands on the Puerto Rican Bank (Lazell 1983; the third

species on the island, *Sphaerodactylus macrolepis* is not distinct). As Mayr (1963) noted, production of evolutionary novelties or new species in small, isolated populations is a rare event; if the initiating genetic events are stochastic in nature, it is highly unlikely that, of all the many islands on the Bank inhabited by *Mabuya* (Fig. 5) and *A. cristatellus* (MacLean 1982, Mayer 1989), these events should occur in both taxa on the same island. We infer that there is something about Carrot Rock itself which is conducive to divergence, rather than that there have been two independent occurrences of a rare stochastic event. We can only suggest that it is the unusual environmental conditions of the island (see above under *Ecology*) that are the common factor in divergence of the two species, but could only speculate about the exact conditions influencing one or the other species. Although it is often argued that evolution proceeds faster in smaller populations, adaptive divergence in fact is faster and greater in larger populations (Weber & Diggins 1990, Coyne et al. 1997), making the situation of two endemic lizards on Carrot Rock even more remarkable.

An alternative explanation for the endemism exhibited by the Carrot Rock saurofauna is that they are relicts, stranded there by post-glacial sea level rise. While we cannot definitively rule out this possibility, the close proximity and very recent separation of Carrot Rock from the main body of the Virgins, and its small size, make it an unlikely refuge for species which have elsewhere gone extinct. Three distributional patterns in the Virgin Islands herpetofauna suggest a relictual distribution, but none match that of the Carrot Rock endemics. *Sphaerodactylus townsendi*, an otherwise Puerto Rican species, occurs in the Virgins only on Frenchcap Cay (Heatwole et al. 1981), but this cay, separated by depths of 22 m, was the earliest of the Virgins to be isolated, about 8000 yr ago when Puerto Rican forms apparently ranged further east on the then exposed bank. Sev-

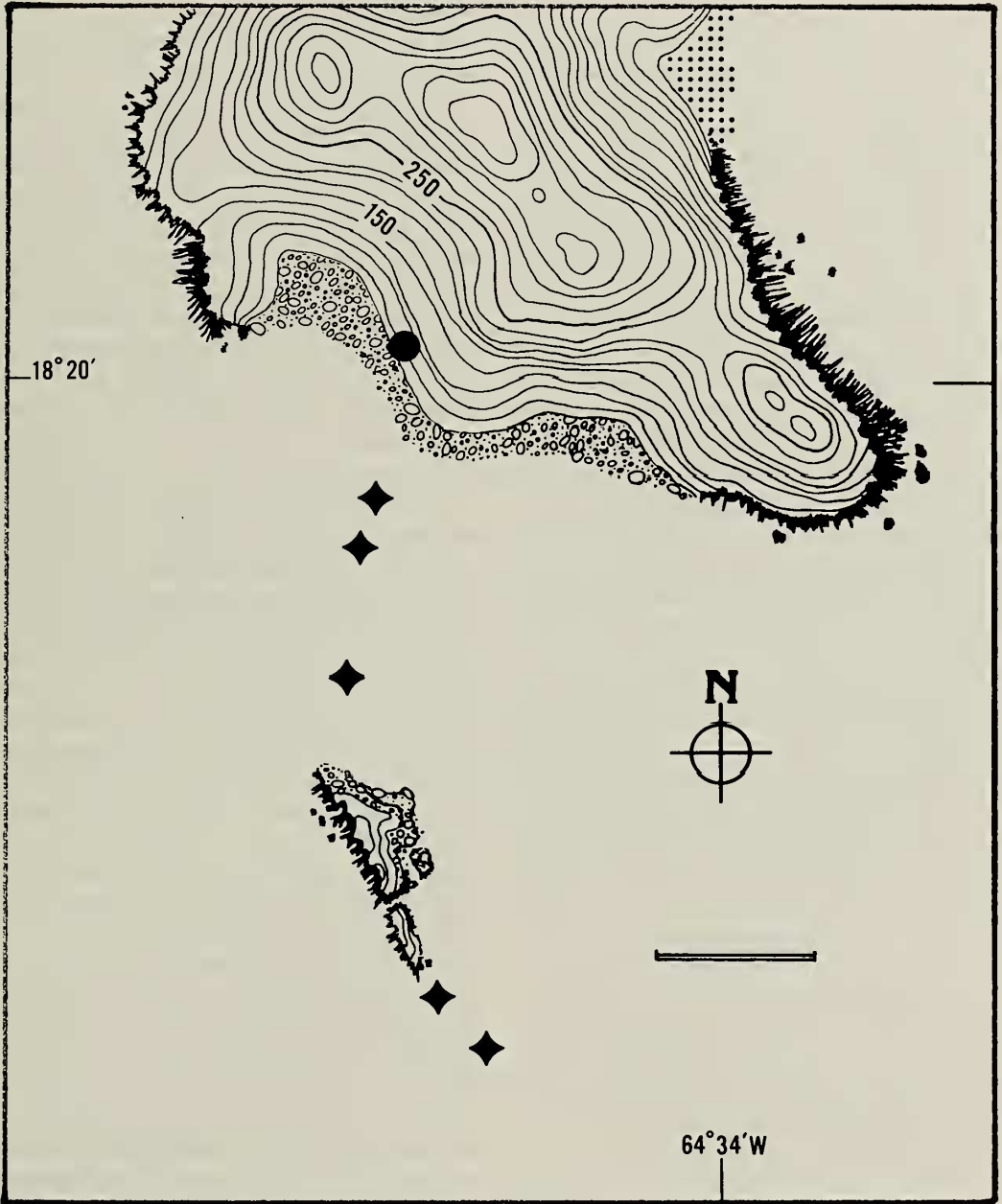


Fig. 6. The south end of Peter Island and Carrot Rock, British Virgin Islands. Dot indicates collection site of *Mabuya s. sloanii*, MCZ 182273, at Stoney Bay. Sand (dots), cobble and scree, and cliffed shorelines are indicated. Black diamonds indicate rocks that break at low water (from U.S. NOAA chart 25641, 1984). Contours are at ca 7.62 m or 25 ft. (from British Directorate of Overseas Surveys 346, Series E 837, 1959). Bar, lower right, indicates 200m.

eral species (e.g. *Anolis roosevelti*) which occur today on only one or a few islands, although they must have once occurred more widely when sea levels were low, have persisted on the largest islands (Mayer 1989). Finally, several species have disappeared from some larger islands while persisting on some smaller islands (e.g., *Alsophis portoricensis*), but such distributions have resulted from anthropogenic extirpations (Barbour 1930, Mayer & Lazell 1988). The Carrot Rock endemics fit none of these patterns. Furthermore, since close relatives of each are present on Peter Island and throughout the archipelago, supposing that they are pre-sea level rise relicts makes their divergence even more remarkable, or merely pushes the time, but not the mode, of their origin to an earlier glacial cycle. For these reasons, we favor the hypothesis of in situ post-glacial divergence (Lazell 1999).

Nomenclature.—Dunn (1936) referred all Antillean skinks (except *lineolata* of Hispaniola) to the species *Mabuya mabouya* Lacépède (1788), which species he also considered to be widely distributed on the mainland, from Mexico through much of South America. Since then, various authors have studied components of this widespread species or species-group, naming or reviving species as needed, and leaving behind an unstudied residue, to which the name *Mabuya mabouya* might continue to be attached (e.g., Rebouças-Spieker 1974, 1981a, 1981b, Avila-Pires 1995). Lacépède's work, however, is not binominal in its nomenclature, and the name, "mabouya" is thus not available.

Throughout the text of his work, Lacépède uses vernacular names, mostly in French, but some, like "Le Mabouya," deriving from other languages. Some Latin names appear in his "Synopsis methodica," but this is not a table of Linnaean-style binomina, but rather a partial translation into Latin of vernacular names given in the text: French vernacular names are translated, but non-French vernacular names appear un-

changed in the "Synopsis". Thus, the French "Le Sourcilleux" of the text appears as "L[acertus]. superciliosus" in the "Synopsis," while "Le Mabouya" of the text appears simply as "Mabouya," as do other non-French vernaculars such as "Jackie" and "Sheltopusik". Names in the table may be uninominal, binominal, or trinominal. Thus "Le Gecko" of the text appears as "Gecko" in the "Synopsis," "La Salamandre terrestre" as "Salamandra terrestris," and "Tortue marin comun" as "T[estudo]. marinus vulgaris".

Although the word "Lacertus" appears as the name of a "genus" in the heading of the "Synopsis," it cannot be read into the remainder of the table so as to turn uninomina into binomina. (Doing so would also turn some binomina in the table into trinomina.) Those names in the table to which Lacépède attached "Lacertus" are specifically listed as such in the table, most often by prefacing the name with "L.". The rule he generally followed is that when the French name is translated as a Latin adjective, it receives the "Lacertus" appellation (e.g., "Le Silloné" of the text becomes "L[acertus]. sulcatus" in the table), whereas names translated as Latin nouns do not (e.g., "Le Dragon" becomes "Draco"); the latter are thus truly uninominal.

In his genus "Lacertus," Lacépède had 26 uninominal and 30 binominal species names; in his genus "Testudo," he had four uninominal, 19 binominal and one trinominal; and similarly for his other genera. Lacépède's work is thus clearly non-binominal, and must be rejected for the purposes of zoological nomenclature. Brongersma (1972), Vanzolini (1977), Savage (1981), Melville (1986), and Smith (1986) also argued that Lacépède was non-binominal, and should be rejected for nomenclatural purposes, and the Commission agreed (International Commission on Zoological Nomenclature 1987). Unfortunately, all these authors but Vanzolini restricted their attention to Lacépède's second volume, on serpents, so that his quadrupeds have not been

formally rejected. Fortunately, rejection of non-binominal works is automatic under the Code, so action by the Commission is not required.

Lacépède's concept of "Le Mabouya" was composite and confused, with no specific locality. Although largely based on Antillean lizards, he also included Sardinia in its range, and the accompanying figure (pl. XXIV) is not even a *Mabuya*; it appears to be, as surmized by Duméril & Bibron (1839), *Chalcides ocellatus*, which occurs on Sardinia. Losing Lacépède's non-binominal name of dubious application will be no loss.

Recently, some authors (Powell et al. 1996, Hedges 1996, Murphy 1996, Powell et al. 1999, Crother 1999), perhaps aware of the difficulties with Lacépède, have begun using the specific name *bistriata* Spix, 1825 (type locality Belém, Brazil) for Antillean skinks previously (e.g., Schwartz & Henderson 1991) referred to *mabouya*. However, even if the Antillean and Brazilian forms are conspecific, which we consider unlikely, *sloanii* predates *bistriata* by 23 years, and the latter name should not be used.

We thus have not used "mabouya" here for Antillean skinks, but rather use Daudin's (1802; Fig. 4) *sloanii* as the first available name, the type of which still exists (Muséum National d'Histoire Naturelle, Paris 554), has good locality data (St. Thomas), and has been examined for us by G. R. Zug. The Antillean skinks formerly included in the *Mabuya* "mabouya" complex not dealt with in this paper (Lesser Antilles, Jamaica, Hispaniola) are best referred to as the *Mabuya sloanii* complex until their systematics can be resolved.

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Appendix I

Material Examined

Islands in the Puerto Rican area are listed in a roughly west to east sequence, and may be located through reference to the maps in Heatwole et al. (1981) and Lazell (1983), and the gazetteer in Mayer (1989). Numbers in parentheses indicate the number of specimens catalogued as a lot. University of Kansas Museum of Natural History (KU) numbers preceded by a letter are from the Albert Schwartz Field Series.

Mabuya sloanii nitida.—Puerto Rico: AMNH 6462, 14007; MCZ 6050, 6052 (2); UMMZ 73828.

M. s. nitida × *sloanii*.—Puerto Rico: UMMZ 73829. Cayo Icacos: MCZ 36624.

Mabuya sloanii sloanii.—Mona: AMNH 13703, 31896, 31908, 115437; Carnegie Museum (CM) 23774-6; Field Museum of Natural History 215, 134332; UMMZ 73817 (3), 73818 (3), 73824 (15), 73825 (2), 124819; National Museum of Natural History (USNM) 133683. Desecheo: USNM 220995. Culebra: AMNH 14005-6, 32910; UMMZ 73819 (13), 73820 (7), 73822 (16), 73823 (10), 73826 (3); USNM 49586. Cayo Luis Peña: UMMZ 73827. Cayo Norte: University of Puerto Rico Rio Piedras. Culebrita: UMMZ 80786. St. Thomas: MNHN 554, 1088 (by G. R. Zug). Saba Island (off St. Thomas): UMMZ 80580; USNM 304553. Water Island: KU V7409. Buck Island (off St. Thomas): UMMZ 73821 (2), 80585. South Ca-pella Island (adjacent to Buck Island off St. Thomas):

UMMZ 80586. Little Tobago: MCZ 158940. Tortola: AMNH 99522. Guana Island: MCZ 166975, 170883; UMMZ 200131; USNM 306182. Great Camanoe: KU V3982. Peter Island: MCZ 182273. Norman Island: USNM 304551. Virgin Gorda: UMMZ 80581, 80582 (3), 80584. Salt Island: UMMZ 74427. Ginger Island: USNM 304550. Prickly Pear Island: USNM 304552. Necker Island: MCZ 176331. Anegada: AMNH 99523-4; CM 17357-8; UMMZ 80583 (28).

Mabuya sloanii complex from Caicos Bank.—Long Cay AMNH 80125-30; MCZ 182881. Six Hill Cays: 117394-6. West Caicos: UMMZ 117392-3.

Mabuya pergravis.—Providencia: Academy of Nat-ural Sciences, Philadelphia 25791-95. San Andrés: UMMZ 127884.